Influence of Maternal Age on the Fitness of Progeny in the Rice Weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae)

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ABSTRACT We studied the effects of maternal age on fitness of progeny in the rice weevil, *Sitophilus oryzae* L. (Coleoptera: Curculionidae). Five-, 20-, and 50-d-old female rice weevils were used to study the effects of maternal age on the lifetime fecundity and longevity of their daughters. In addition, we determined the effects of maternal age on the weight and survivorship of daughters' progeny. Daughters of 5- and 20-d-old weevils lived longer, and the numbers and weights of the progeny of these daughters were higher than for daughters of 50-d-old weevils. Survivorship of immature grand-offspring of 5-, 20-, and 50-d-old female weevils was similar. None of the fitness characteristics of the daughters and grand-offspring of 5- and 20-d-old weevils that were measured differed significantly. We believe maternal age effects on rice weevil progeny fitness may at least partly be acting through maternal age effect on egg size. Individuals that developed from younger 5- and 20-d-old weevils had a greater fitness than those produced by older 50-d-old females. Our study shows maternal age is impacting life history parameters that influence population dynamics across generations. Therefore, maternal age could significantly affect population development and have far reaching implications for pest management and simulation modeling of rice weevil populations.

KEY WORDS rice weevils, egg size variation, maternal age, offspring fitness, "Lansing effect"

A decline in offspring fitness with maternal age is common in insects (Parsons 1964, Mousseau and Dingle 1991). Studies have shown that progeny of older mothers have higher mortality, longer larval development times, and are much smaller at adult emergence compared with progeny from younger mothers (Mousseau and Dingle 1991, Kern et al. 2001 and references therein). Many other studies have shown that, in insects, there is a decrease in egg size with maternal age (Fox 1993 and references therein, Perez-Mendoza et al. 2004). In the case of Perez-Mendoza et al. (2004), this decrease in egg size was striking in that eggs produced by mated 5-d-old rice weevil, *Sitophilus oryzae* L. (Coleoptera: Curculionidae), females were 20% larger than eggs produced by mated 10- to 20-d-old females and ≈250% larger than eggs produced by mated 50- to 60-d-old females. The decline of both offspring fitness and egg size with maternal age has led to the suggestion that maternal age may influence offspring fitness via maternal age effects on egg size (Fox 1993).

A reduction in offspring fitness with maternal age suggests that information on changes in the maternal environment as females age is being transmitted to offspring, possibly through egg size (Rossiter 1991a, b, Rossiter et al. 1993, Rolff 1999). Such transfer of information from the maternal environment to the phenotype of offspring is referred to as non-Mendelian maternal effect (Mousseau and Fox 1998). More generally, maternal effect refers to all non-Mendelian parental effects of both maternal and paternal origin (Hunter 2002). Manifestation of maternal effects can occur within the lifetime of an organism or across generations and could potentially have great significance for population dynamics (Beckerman et al. 2002). Maternal effects can affect population dynamics (Wellington 1957, Leslie 1959, Benton et al. 2001, Beckerman et al. 2002, Hunter 2002) through their influence on life history traits, such as survival, dispersal, growth rate, diapause, and fecundity (Hunter 2002). Therefore, omission of maternal effects in models used to predict population dynamics may result in poor predictions (Benton et al. 2001).

Apart from the study by Perez-Mendoza et al. (2004), no other research on maternal effects in rice weevils has been conducted. The marked reduction in egg size with age in rice weevil females (Perez-Mendoza et al. 2004) suggests the possible existence of maternal effects that could influence population dynamics in this species. Therefore, our objective was to determine the effects of maternal age on the fitness of rice weevil progeny. Based on the findings of Perez-Mendoza et al. (2004), younger rice weevil females

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would be expected to produce offspring that are more fit than older weevils. We hypothesized that progeny produced by mated 5-d-old female rice weevils have a greater fitness, that is, they live longer and produce a larger number of progeny that are heavier and have greater survivorship than progeny produced by older mated females.

Materials and Methods

Most of the experiment was conducted in a chamber maintained at 30 ± 1°C with a 12:12 L:D photoperiod, because these are optimal conditions for rice weevil population development. Within the chamber, relative humidity was controlled by placing cages containing insects on a perforated false floor in a plastic box (40 by 27.5 by 16 cm high) containing saturated NaCl solution below the false floor to maintain 75% RH (Greenspan 1977). These environmental conditions were used for all phases of the study, except while G1 weevils were paired and being aged to the appropriate treatment age (5, 20, and 50 d old). While paired, the boxes contained a saturated sodium bromide (NaBr) solution below the false floors to maintain 56% RH (Greenspan 1977), and the vials were placed in a chamber held at 25 ± 1°C with a 12:12 L:D photoperiod. Weevils were kept at these modified environmental conditions during pairing because they are the conditions Perez-Mendoza et al. (2004) used to age weevils during their study, and we wanted to duplicate their conditions during aging.

We used whole kernel, hard red winter wheat, *Triticum aestivum* L., throughout the study. We ensured that wheat kernels used in the study were of uniform size because kernel size may have an effect on the fitness of weevils developing inside them (Shazali, 1986, Campbell, 2002). Kernels of uniform size were obtained by sieving a group of kernels first using a U.S. Standard no. 6 sieve; kernels that passed through this sieve were collected and sieved using a no. 8 sieve. Kernels remaining on the no. 8 sieve were of uniform size (average weight, 33.2 ± 0.7 [SE] mg) and were used in the study. Kernels of uniform size required for the entire study were obtained at the same time from the same wheat supply. Altogether, 18 cages with 200 g of kernels of uniform size in each were obtained during a single sieving event. Kernels that were not immediately needed were kept in a refrigerator at 5 ± 1°C until required. When kernels were needed, they were equilibrated to 14.5% moisture content over a 6-wk period before use.

Mated, 50-d-old, G1 Female Treatment (50-d-old Treatment). Parents (parental generation) of 50-d-old female rice weevils were derived from a laboratory strain reared on whole kernel wheat. These parents were obtained by clearing wheat (removing all adult weevils) in six 800-ml jars used to culture weevils and letting adults emerge over a 3-d period (Table 1; days −103 to −100). These adults were then held in three 800-ml jars, each containing 200 ± 1 g of uninfested wheat, for 2 wk. On day −86, 200 2-wk-old adults were placed in each of three cylindrical cages (8.5 cm by 8 cm high) with screen bases and lids. Each of the cages contained 200 ± 1 g of wheat (14.5% moisture content); all cages were placed on a perforated false floor in a plastic box containing saturated NaCl solution. We used 2-wk-old females to maximize egg-laying and increase the probability of getting a large number of pupae of similar size that would ultimately be used to obtain females of a standard age.

All parental adults in each of the three cylindrical cages were removed from the cages after 4 d (day −82). In each cage, kernels containing weevil pupae were detected by X-ray analysis (Throne 1994) 24 d later (day −58). X-raying was accomplished by placing infested kernels in a single layer on sheets of cellulose (previously exposed 13 by 18-cm radiographs) coated with double-stick tape. A sheet of wheat kernels was placed on a sheet of film (Kodak Industrex M X-ray film in Ready Pack II foil packs; Eastman Kodak, Rochester, NY) placed 56 cm below an X-ray source (model 43855A Faxitron; Hewlett–Packard, McMinnville, OR) and exposed for 3 min at 18 kV and 3 mA. Negatives were examined under a stereomicroscope at a minimum of ×12 magnification for the presence of weevil pupae. Six hundred kernels containing pupae were identified and placed individually in 13 by 100-mm glass tubes with cotton wool plugs and were checked daily for adult emergence. Preliminary experiments had indicated that at these environmental conditions, the peak of adult emergence was on days 30 and 31 after parental adults were removed. Therefore, only individuals emerging 30 and 31 d later were sexed (Halstead 1962), and females found were weighed to the nearest 0.1 μg using a Mettler UMT2 balance (Columbus, OH) and used to form pairs with 2-wk-old males (day −50). Using only females that emerged during a 2-d window of emergence ensured that females used to make pairs were of similar age.

The 2-wk-old males used to form pairs with generation one (G1) females were obtained from the same colony. These males were obtained by clearing wheat in three 800-ml jars used to hold weevils started at the same time and letting adults emerge over a 3-d period. These adults were sexed, and males were held in an 800-ml jar containing 200 ± 1 g of uninfested wheat for 2 wk. Before pair formation, an elytron of each male was marked using white nail polish for easy identification. Males of the same age were used because paternal age could influence offspring fitness. Priest et al. (2002) have shown that paternal age affects offspring longevity and mortality trajectories in *Drosophila melanogaster*.

Male and female pairs were individually placed in labeled plastic vials (3.2 by 8 cm), with snap-cap screen lids, and containing 10 g of uninfested wheat. Vials were placed on perforated false floors in plastic boxes. We aged these pairs for 50 d at 25°C and 56% RH. Twenty-five days starting from when pairs were first formed, each pair of weevils was transferred into a new vial containing 10 g of uninfested wheat (day −25). After an additional 24 d, the female of each pair was transferred into a new vial containing 5 g of wheat,

Table 1. Steps followed during the experiment and the time when they occurred relative to the mid-point of the 48-h egg-laying period and trio formation

Day	Treatment		
	50 d old	20 d old	5 d old
−103	Culture jars cleared of adults		
−100	Adults removed to new wheat to age for 2 wk		
−86	200 2-wk-old adults moved to 200 g wheat to oviposit		
−82	Adults removed from wheat		
−72		Culture jars cleared of adults	
−69		Adults removed to new wheat to age for 2 wk	
−58	Wheat X-rayed and pupae separated		
−57			Culture jars cleared of adults
−55		200 2-wk-old adults moved to 200 g wheat to oviposit	
−54			Adults removed to new wheat to age for 2 wk
−51		Adults removed from wheat	
−50	G1 pair formation		
−40			200 2-wk-old adults moved to 200 g wheat to oviposit
−36			Adults removed from wheat
−27		Wheat x-rayed and pupae separated	
−20		G1 pair formation	
−25	Transfer pairs to new wheat		
−12			Wheat X-rayed and pupae separated
−5			G1 pair formation
		All treatments on same schedule starting on day −1	
−1		Transfer females to new wheat	
0		Mid-point of 48-h egg laying period	
1		Remove females	
26		Wheat x-rayed and pupae separated	
T0			Trio formation
T15			Transfer trios to new wheat
T30	Repeat transfer to new wheat every 15 d, and start sieving old wheat daily for G3 progeny		
T135			Last transfer of trios; all females dead on day T150

Trios with G2 females set up as adults emerged, so day T0 varied among trios and day numbering restarted.

and the male was discarded (day −1). The vials were placed in another plastic box containing a saturated NaCl solution, and the box was kept in a chamber maintained at 30 ± 1°C. After 48 h, the females were removed from the vials, and discarded (day 1). The duration from the time when pairs were first formed until the mid-point of the 48-h egg-laying period (day 0) was 50 d, so the G1 females were now 50 d old. The mid-point of the 48-h G1 female egg laying period was coordinated to be the same in all the treatments (5-, 20-, and 50-d-old females).

In each vial, kernels containing weevil pupae were detected by X-ray analysis (Throne 1994) 26 d later (day 26). From each vial, 10 kernels containing G2 pupae were placed individually in labeled 13 by 100-mm glass tubes, and tubes were checked daily for G2 adult emergence. Emerging G2 weevils from each G1 female were sexed. For each G1 female, a single G2 female was randomly chosen. This female, together with two 2-wk-old males, obtained from the same colony, were placed in a plastic vial (3.2 by 8 cm with a snap-cap screen lid) that contained 10 g of uninfested wheat (day T0 – day when trios were formed). Two males were used to reduce the probability of a female having no male to mate with in case one died. Forty-three G2 females were used to form trios for this treatment.

Fifteen days after trio formation (day T15), each trio was transferred into a new vial containing 10 g of uninfested wheat. During the transfer, any dead weevil found was sexed. If a dead male was found during a wheat change, it was replaced with another male of a similar age— usually obtained from vials where the G2 female in the trio had died. If a dead female was found, that trio was terminated. On average, males and females died at a rate of 9 and 12, respectively, per wheat change period. Wheat from the 43 vials where the trios were previously held (old vials) was sieved daily starting immediately after the trios were removed, and any adult weevils found were removed and immediately sexed and weighed to the nearest 0.1 μg using a Mettler UMT2 balance. Wheat was sieved daily to minimize the possibility of G3 weevils laying eggs and confounding data. Sieving of each sample was terminated when no further G3 adult emergence occurred over a 10-d sieving period.

The process of transferring weevils to new wheat was repeated every 15 d until all the G2 females used to form trios died (days T30–T135). During this study, there was a maximum of nine transfers, and these were

numbered 1–9. The wheat transfer number (period) when each G2 female was found dead was noted. All sieved wheat associated with each G2 female was kept together in a ziplock bag; this wheat was X-rayed after all the sieving was completed to determine the extent of immature G3 weevil mortality.

In later weevil transfers, some of the old vials that were sieved daily produced no G3 weevils. In such cases, wheat was sieved for 40 d.

Mated, 20-d-old, G1 Female Treatment (20-d-old Treatment). On day −55 (Table 1), 200 2-wk-old adults (parents of 20-d-old females) were placed in each of three cylindrical cages (8.5 cm by 8 cm high) with screen bases and lids. Steps described in the 50-d-old treatment were repeated to obtain 2-wk-old male and G1 female pairs. The culture jars used to obtain G1 adults were a different set than those used for the 50-d-old treatment. Nineteen days after pairs were formed, the G1 female of each pair was transferred into a new vial (day −1). After 48 h, all the females were removed from the vials (day 1). The duration from when pairs were formed until the midpoint of the 48-h egg-laying period (day 0) was 20 d, and the G1 females were now 20 d old. After this point, all the procedures described in the 50-d-old treatment were also applied to the 20-d-old treatment. Thirty-five G2 females were used to form trios for this treatment (day T0).

Mated, 5-d-old, G1 Female Treatment (5-d-old Treatment). On day −40 (Table 1), 200 2-wk-old adults (parents of 5-d-old females) were placed in each of three cylindrical cages (8.5 cm by 8 cm high) with screen bases and lids. Steps described in the 50-d-old treatment were repeated to obtain 2-wk-old male and G1 female pairs. The culture jars used to obtain G1 adults were a different set than those used for the 50- and 20-d-old treatments. Four days after pairs were formed, the G1 female of each pair was transferred into a new vial (day −1). After 48 h, all the females were removed from the vials (day 1). The duration from when pairs were formed until the midpoint of the 48-h egg-laying period (day 0) was 5 d, and the G1 females were now 5 d old. After this point, all the procedures described in the 50-d-old treatment were also applied to the 20-d-old treatment. Thirty-five G2 females were used to form trios for this treatment (day T0).

Statistical Analyses. Vials containing G2 females (trios) from all the three treatments were placed randomly in three plastic boxes. The design for data analysis was a randomized complete block design (RCBD) with the box in which G2 females were kept considered as the block. All statistical procedures were accomplished using Statistical Analysis System software (SAS Institute 2001). PROC GLM was used to run analysis of variance (ANOVA) to determine whether the weights of G1 females differed and the effects of treatment on the (1) longevity of G2 females, (2) lifetime fecundity of G2 females, and (3) mortality of immature G3 progeny. In addition, PROC GLM was used to run ANOVA to determine the effects of treatment and sex on the weight of G3 progeny. Where data (z) were weevil numbers, the $\log(z + 1)$ transformation was first used to stabilize variances before analysis. The longevity of G2 female weevils was assessed by assigning each weevil a score based on the wheat change period when its carcass was found. For example, a weevil whose carcass was found during the eighth wheat change was assigned a score of 8; this implied it lived longer than a weevil whose carcass was found, for example, during the fourth wheat change and would have a score of 4. The normality of scores was first tested using PROC UNIVARIATE before PROC GLM was used to run ANOVA. Because G2 females were transferred to new wheat to lay eggs every 15 d, it was not possible to exactly pinpoint when a G2 female died; therefore, analysis of the effects of treatment on longevity of G2 females could not be conducted using number of days lived as a response variable. However, an estimate of the number of days each G2 female lived can be obtained by multiplying the assigned score by 15. In the analysis of mortality of immature G3 progeny, proportion of dead immatures [(number of dead immatures)/(number of dead immatures + number of weevils that emerged)] was used. Arcsine transformation was used to stabilize variances before analysis.

We tested for the effects of treatment on sex ratio using the number of G3 progeny produced by each G2 female. We created the response variable "deviation" (proportion of females produced by each G2 − 0.5). We argued that any deviation from 0 would indicate that the ratio is not 1:1. PROC GLM was used to run ANOVA to test for the effects of treatment on deviation; we determined whether deviation was significantly different from 0 (whether the sex ratio was1:1) by looking at the test for LSMEANS = 0.

Results

Effects of Different G1 Female Initiation Dates on Weight of G1 Females. G1 females in the 5-, 20-, and 50-d-old treatments had similar weight ($F = 0.18$; df = 2,296; $P = 0.84$); the average weights were 2.33 ± 0.03, 2.35 ± 0.03, and 2.32 ± 0.02 (SE) mg, respectively. This indicated our methods of manipulating maternal age seem to have had no effect on the quality of G1 mothers, and the effects of possible colony cycling did not confound those of maternal age.

Effects of Maternal Age on the Number of G3 Progeny Produced (Grand-offspring). Daughters of 5- and 20-d-old females produced about twice as many progeny than daughters of 50-d-old weevils (Table 2; $F = 26.5$; df = 2,4; $P < 0.001$). Maternal age had no effect on sex ratio of G3 progeny ($F = 0.86$; df = 2,4; $P = 0.49$), and the sex ratio in all three treatments did not differ from 1:1. *P* values for the LSMEANS = 0 test (1:1 sex ratio test) were 0.73, 0.17, and 0.83, respectively, for the 5-, 20-, and 50-d-old treatments (Table 2).

Effects of Maternal Age and Sex on the Weight of G3 Progeny. G3 progeny produced by daughters of 5- and 20-d-old females weighed slightly more than those produced by daughters of 50-d-old females (Table 2; $F = 7.34$; df = 2,188; $P < 0.01$). Females were heavier

Table 2. Effects of maternal age on fitness (mean ± SE) of G2 daughters and G3 progeny

Maternal age (days)	Longevity[a] of G2 daughters	Number of G3 progeny produced	Weight of G3 progeny (mg)	Proportion mortality of G3 immatures	Sex ratio deviation[b]
5	4.91 ± 0.29a	105.4 ± 11.1a	1.89 ± 0.012a	0.151 ± 0.03a	−0.0024 ± 0.02a
20	4.83 ± 0.31a	91.6 ± 12.6a	1.92 ± 0.013a	0.103 ± 0.03a	−0.037 ± 0.02a
50	3.47 ± 0.31b	50.7 ± 8.2b	1.85 ± 0.014b	0.121 ± 0.02a	−0.0072 ± 0.01a

Means within a column followed by the same letter are not significantly different.

[a] The longevity of G2 female weevils was assessed by assigning each weevil a score based on the wheat change period when its carcass was found. An estimate of longevity in days can be obtained by multiplying the longevity score by 15.

[b] Deviation is equal to proportion of females produced by each G2 − 0.5.

than males ($F = 23.8$; df = 1,188; $P < 0.01$). The average weights of G3 males and females were 1.85 ± 0.01 and 1.93 ± 0.01 mg, respectively. There was no interaction between maternal age and G3 progeny sex ($F = 0.24$; df = 2,188; $P = 0.79$).

Effects of Maternal Age on Mortality of G3 Immature Stages. G3 immatures in the 5-, 20-, and 50-d-old treatments had similar mortality ($F = 0.31$; df = 2,4; $P = 0.75$).

Effects of Maternal Age on the Longevity of G2 Female Progeny. The kurtosis value for longevity scores assigned to weevils was −0.85, indicating that the scores did not differ from a normal distribution. G2 daughters produced by 5- and 20-d-old females lived ≈30% longer than those produced by 50-d-old females (Table 2; $F = 107.3$; df = 2,4; $P < 0.01$).

Discussion

Our study has shown that, in *S. oryzae*, maternal effects have influence on life history parameters that affect population dynamics. Daughters of 5- and 20-d-old weevils lived longer, and the numbers and weights of the progeny of these daughters were greater than those of daughters of 50-d-old weevils. None of the fitness characteristics of the daughters and grand-offspring of 5- and 20-d-old weevils that were measured differed significantly. Survivorship of immature grand-offspring of 5-, 20-, and 50-d-old female weevils was similar.

It is feasible that the higher lifetime fecundity of daughters of 5-and 20-d-old weevils may partly be caused by their longevity being greater than that of daughters of 50-d-old weevils—daughters of younger females lived ≈30% longer than those of older females but laid about twice as many eggs. The greater longevity of offspring from younger mothers compared with those from older mothers is known as the "Lansing effect," a phrase derived from the work of Lansing (1947, 1948, 1954) on Rotifers. "Lansing effect" has also been found in several other taxa (Priest et al. 2002).

The fact that granddaughters of 5- and 20-d-old weevils were heavier than those of 50-d-old weevils shows that maternal effects in rice weevils can be transmitted across two generations. This maternal effect would also be expected to impact population dynamics, because egg size and egg number are generally correlated with body size (Fleming and Gross 1990, Kawecki 1995).

The similarity in survivorship of immatures from G2 mothers belonging to the 5-, 20-, and 50-d-old female treatments may be a result of significantly greater longevity of G2 females in 5- and 20-d-old treatments. If a comparison of survivorship of immatures of G2 mothers of the same age were possible among the 5-, 20-, and 50-d-old treatments, we would expect that offspring of G2 mothers in the 50-d-old treatment to experience lower survivorship than those of G2 mothers in the 5- and 20-d-old treatments. This is likely the case because all other fitness parameters measured indicate a decline in fitness of progeny in the 50-d-old treatment, and this is also supported by the work of Kern et al. (2001), who showed that egg hatching success and larval viability declines with mother's age in *D. melanogaster*. However, the similarity in survivorship of immature offspring of G2 mothers in the three treatments that we found may be because G2 mothers in the 5- and 20-d-old treatments live much longer, and the effects of age would result in the production of a higher number of less fit progeny late in the G2 mothers lives.

Based on the work of Perez-Mendoza et al. (2004), rice weevil egg size unequivocally decreases with maternal age. During this study, we did not measure the size of eggs laid by weevils of different ages; therefore, we could not separate the effects of increasing maternal age from decreasing egg size. However, we hypothesize that if female age were controlled, size differences in eggs laid by weevils of a given age would not be large enough to result in detectable differences in fitness such as those we observed in this study. This is based on the fact that there is extremely low variability in the size of eggs laid by rice weevil females of the same age (Perez-Mendoza et al. 2004) and the observation that individuals developing from eggs of 5- and 20-d-old weevils have similar fitness, despite eggs of 5-d-old weevils being 20% larger than those of 20-d-old weevils. Therefore, we suggest it is not practical to separate the effects of increasing maternal age from decreasing egg size. Despite this, the work of Perez-Mendoza et al. (2004) leads us to conclude that maternal age effects on progeny fitness observed in our study could be acting through maternal age effect on egg size. Our situation is similar to that in a study by Fox (1993), where egg size was not independent of maternal age, and it was not possible to test whether egg size was responsible for the reduction in offspring fitness with maternal age; however, he concluded that the reduction in offspring fitness with

maternal age was most likely a result of smaller eggs laid by older females, possibly interacting with change in egg quality.

Our study shows that the effects of maternal age in rice weevils can be transferred across generations and could have great significance for population dynamics (Beckerman et al. 2002). Maternal effects influence population dynamics by causing phenotypic traits expressed by individuals within populations to vary among generations, resulting in variable response to environmental challenges (Wellington 1957, Leslie 1959). It has been suggested that maternal effects impact population dynamics by acting as one source of both variability and delayed density dependence (Beckerman et al. 2002); the latter can destabilize population dynamics and promote cyclic dynamics (Schaffer and Kot 1986, Turchin 1990, Berryman 1992).

Given the potential impact of maternal age on population dynamics in rice weevils, it may not be accurate to use simple nonstructured (Royama 1992) and age- or stage-structured models (Caswell 2001) to predict population fluctuation in rice weevils, because these models use life history traits such as survival and fecundity that do not vary with time. In these models, only the initial values of survival and fecundity rates control the predicted dynamics of the model population (Beckerman et al. 2002). Inclusion of maternal age effects in population models that have been developed and used to optimize management of insect pests of stored wheat (Hagstrum and Throne 1989, Hagstrum and Flinn 1990) would probably increase their predictive accuracy. This can be done by, for example, altering the fecundity and longevity of offspring from mothers of different ages.

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